

13.

Arithmetical Definition of the Species, Subspecies and Race
Concept, with a Proposal for a Modified Nomenclature.

Containing a simple method for the comparison of related populations.¹

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(Text-figures 1-4).

INTRODUCTION.

Ever since naturalists began to doubt the special creation of species, in consequence of the accumulating incontrovertible evidence proving the descent of species from preexisting forms of life, the question of what constitutes a species became bothersome. The acuteness of the problem was intensified when biologists ceased to be satisfied with describing and cataloging species of plants and animals by a study of one or but a few specimens, and began to study in detail the individuals comprising a species *en masse*. The great individual variability of the characters employed for specific distinctions and the consequent difficulty of drawing sharp lines of demarcation between closely related species was thus revealed.

This fundamental problem in biology engaged the attention of students and a considerable literature has grown up dealing with the question of what constitutes a species. A good deal of what has been written has reference to its speculative aspects. It is not the aim of this article to add anything to the purely abstract discussions of the problem. Instead, it represents an attempt to solve this problem and determine definitely just what is a species by reference to a series of actual data. It is my intention to consider in detail a number of concrete cases showing the facts of speciation as they occur in nature and an attempt is made to correlate the facts and draw the proper conclusions therefrom.

The data employed to support the propositions advanced in the present paper are entirely taken from populations of fishes. The data were not specially collected for this paper, but have been gathered in connection with my revisional studies of American fishes. Some of the data have been published in reports on these studies; others are here published for the first time, or previously published data are amplified. As far as the included evidence is concerned this paper may be said to be a sort of a by-product of my revisional studies of the genera of American fishes, and the supporting data presented below have been only casually selected to prove the propositions advanced. While the examples cited have been taken entirely from the class of fishes, the same method no doubt will be found applicable to other groups of animals, and plants as well.

All the examples included below are based on quantitative characters. The method developed here is most strikingly applicable to such characters

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which thus serve best for the purpose of illustration. For some specific characters this method will be applied with greater difficulty and a lesser degree of precision, and cases may be encountered in which it is inapplicable, especially in cases in which differences are based on qualitative characters (see below). However, this is a problem in practical usage. Such cases must be considered by themselves, and special means of expressing particular characters in the form of frequency distributions, may be devised. The fact that this method may be inapplicable practically in some cases does not detract from the pertinence of the general principles evolved as a result of its application in the great number of cases in which it may be used with ease and precision.

The question of what constitutes a species cannot be considered by itself. To solve this problem consistently it must be broadened to include the subdivisions of the species, since, as will be shown definitely hereafter, the different categories which may be established imperceptibly grade into one another. This paper, therefore, goes into the whole problem of the species and its subdivisions. In connection with this study the question of the nomenclature of taxonomic categories below specific rank is examined and a modification of the method now in general use, is proposed. A simple method for the comparison of closely related populations is employed in this paper, which may prove to be a useful tool in the taxonomic study of populations of specific or lower rank.

FAILURE OF PREVIOUS ATTEMPTS TO ESTABLISH ABSOLUTE LIMITS TO THE SPECIES CONCEPT.

A number of criteria have been used by previous writers for the purpose of defining and establishing absolute boundaries to limit the species concept. The literature on the subject is quite voluminous, and it is not my present purpose to give a complete review of such previous attempts. This has been done by a number of writers in greater or lesser detail, and the reader may be referred to one of these writers, such as Robson (1928) who also gives an extensive bibliography of the subject. In general, it may be stated that all criteria which have been proposed for establishing absolute boundaries by which we may definitely determine just what constitutes a species, have been found wanting. One of these criteria, the morphological, may be considered here briefly because the definitions proposed herewith are based solely on that criterion. It is the only criterion which is most generally useful in the practice of taxonomy.

A population of variable individuals was considered to be fully distinct specifically from another population differing in at least one structural or color character in such manner that no intergrading individuals occur, but that every single individual may be referred either to one or the other of the two populations. Such populations have been regarded as fully distinct species. Even at the present time some systematists hold to this as a criterion for distinguishing species, or as the most important criterion. However, absolute lack of intergradation in nature is far from being the usual condition. On the contrary, intergradation of related populations is so general that it would not be far fetched to make the statement that it is the rule rather than the exception. Certainly most closely related species of fishes, in my experience, have been found to intergrade more or less.

Specific characters are roughly divisible into two classes: (1) quantitative characters, such as the number of fin rays, scales or vertebrae, proportional measurements, etc.; (2) qualitative, such as differences in color, or the presence or absence of certain structures or color marks, or differences in their form. Among fishes the former is predominant. Qualitative structural characters which are absolute, that is, they practically do not show any intergradation, are in many cases considered to be of

generic or subgeneric, rather than specific, importance. Also, two groups of related species between which a comparatively wide gap exists with respect to a given quantitative character are often placed in separate genera or subgenera. Characters which are considered to be of specific importance only, by general consent, more likely than not, will be found to intergrade between two closely related populations when a sufficiently large number of individuals are studied in detail. This is true not only of quantitative characters, but frequently an imperceptibly gradual intergradation occurs also in the case of qualitative characters, although in the latter case it may be difficult to measure and express in terms of precise figures the degree of intergradation.

The general existence of intergradation is not duly reflected at present in taxonomic works. The reason taxonomists have been able to describe species generally in such manner as to make it appear that no intergrading individuals are present, is that these descriptions are usually based on but a few individuals. Consequently, by the law of chance, such few individuals were apt to fall, in most cases, near the center, and away from the extremes, of a regular frequency distribution. Occasional bothersome specimens may have been explained away as being abnormalities, sports or hybrids. However, such border line specimens will be found in most closely related species if a sufficient number of individuals are studied in detail. Except for possible occasional hybrids, or atypical individuals for various reasons, such specimens are normal individuals, but they fall in at the extreme of the frequency distribution, and as far as any given single character is concerned they may as well belong to one species as to another closely related one.

THE TRUE MORPHOLOGICAL CRITERION IS THE DEGREE OF INTERGRADATION, OR DIVERGENCE.

The intergradation between natural populations varies in degree. When a sufficient number of pairs of closely related populations are compared and the several intergradations, or divergences, are arranged in order of magnitude, we obtain a series that is graduated by virtually infinitesimal steps. It follows, therefore, that the determination of whether a given pair of populations constitute two species or belong to a category of lower rank depends on the *degree* of intergradation; or, to view it from another angle, the *degree* of divergence. As a further consequence, it follows that species as well as subspecies and races are not absolute entities. The lines drawn to limit these classificatory units must be arbitrary. That this is not merely a theory but the actual condition which exists in nature is attempted to be proved in the paragraphs which follow. (I discussed this proposition in another paper (1937a). Data to prove it are presented here.) After adopting a measure by which the degree of intergradation is expressed in terms of a definite figure, a series of data obtained by the study of pairs of closely related populations of fishes is presented and the figure expressing the degree of intergradation for each pair is calculated by the method employed. The figures thus obtained form a gradual series which may be arranged in ascending or descending order and there are no breaks in the gradual continuity of the series where sharp lines may be drawn to limit absolutely our concept of species, subspecies or race.

MEASURE OF INTERGRADATION, OR DIVERGENCE.

Our next step in the solution of the problem is to adopt a definite and uniform measure by which the degree of intergradation, or divergence, between any two closely related populations may be expressed in terms of a *single* figure. Several methods of measuring intergradation or divergence may be employed. For instance, Davenport (1898) proposes what are essen-

tially two methods of measuring precisely the difference between two closely related populations. Davenport represents the two related populations, in every instance cited by him, in the form of a single bimodal curve. One measure which he designates as the "index of divergence" represents "the ratio of the distance between the modes to the half-range . . . of the broader curve." The other measure, designated by the author as the "index of isolation," represents "the ratio of the depression [between the two parts of the bimodal curve] to the length of the shorter mode." (The "depression" is the vertical distance between the apex of the smaller curve and the lowest point of the depression). Both measures are expressed as percentages. A measure which is often employed to indicate the difference or divergence between two populations may be represented by the formula

$$\frac{M_1 - M_2}{\sqrt{E_1^2 + E_2^2}}$$

in which M_1 and M_2 represent the means of the two respective populations, and E_1 and E_2 represent the probable errors of the two means, respectively. This expression represents the ratio of the difference between the means to the probable error of this difference (see Pearl, 1930, pp. 282-287). In treatises dealing with the application of statistical methods to biological problems the statement is often made that when the numerical value of this ratio is 3 or 4, it is "significant." Other methods may be suggested. For our present purpose a simple method of expressing the degree of intergradation, or divergence, between two related populations is proposed to be used as indicated below.

For the present I am not going to discuss in detail the advantages and disadvantages of the various methods which have been proposed or which may be suggested with the method employed herein. This is a problem by itself, a full discussion of which would lead us astray from our main thesis. If any consistent method be adopted and a number of closely related pairs of populations be compared by it, the results quite likely will form a gradual series going to prove the continuity of intergradations, *inter se*, in nature; but the relative position of the pairs of populations compared, in the series, will no doubt change somewhat according to the method used, and some methods will more nearly represent the facts of nature than others. A brief comparison is made below (p. 279) between the method employed herein and the standard method, and it is shown that the latter is not well adapted for our purpose. Besides the fitness of the measure employed to represent the facts more nearly in their true light, it has two salient advantages which may be mentioned briefly. (1) It may be determined easily and quickly, a very desirable consideration, especially from the point of view of the busy taxonomist. (2) Because of its simple character its pertinence in explaining the facts of nature is strikingly evident and the relationship of variable and closely related populations may be appreciated readily when this measure is used.

Our simple measure may be illustrated by the following hypothetical examples. Let us assume two species of fishes, A and B, the chief differentiating character of which is represented by the number of scales in the lateral line, a character which is frequently employed in distinguishing closely related species of fishes. Let us suppose further that the scales of a hundred specimens of each species have been counted, and the figures obtained were as follows:

Number of scales (class)	24	25	26
Species A (frequencies)	92	8	
Species B (frequencies)		97	3

It may be said then that species A intergrades with species B to the extent of 8% and this figure may be suggested as our measure of intergradation.

While this figure obviously suggests itself, it is not the figure finally adopted. The measure of intergradation for the above hypothetical case, by the method employed, is 4%, for reasons which will become clear presently.

In nature examples similar to the above simple hypothetical case may be encountered; but the variability and relationship of closely related natural populations is much more often not as simple. Let us, therefore, take the next step and assume a hypothetical case where the dispersion of the frequency distributions and the overlap are a little more pronounced; while at the same time the frequency distributions are perfectly regular, as follows:

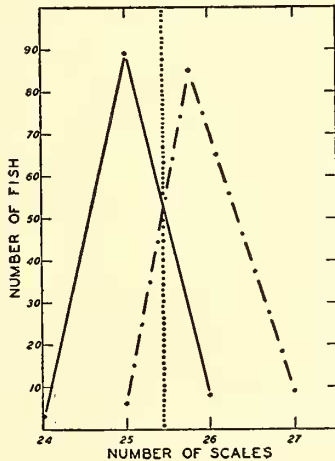
Number of scales (class)	24	25	26	27
Species A (frequencies)	5	90	5	
Species B (frequencies)		5	90	5

In this perfectly regular hypothetical case each species overlaps the other by 5% and this figure may be taken as our measure of intergradation.

Again it may be stated that perfectly regular frequency distributions such as the foregoing hypothetical case are seldom encountered in practice. Frequency distributions are usually irregular or, to use the technical expression, skewed. Part of the irregularity encountered in practice is no doubt due to incomplete sampling of the populations; but it is evident that skewness in the frequency distributions of populations is the more usual and normal condition in nature. Let us then assume a hypothetical case where the frequency distribution is irregular while the overlap is more pronounced than in the simple hypothetical case cited first, as follows:

Number of scales (class)	24	25	26	27
Species A (frequencies)	3	89	8	
Species B (frequencies)		6	85	9

This case is a little more complicated and is nearer the majority of examples encountered in actual practice. How are we to measure intergradation in this case?



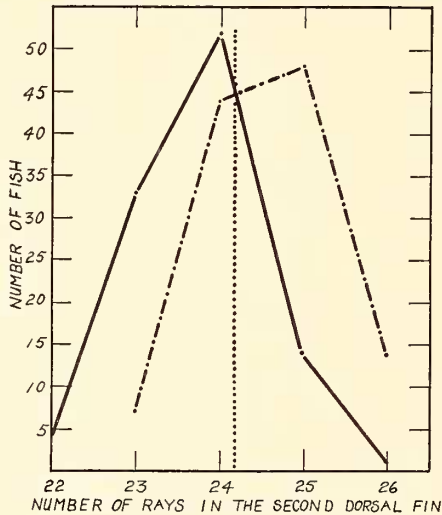
Text-figure 1.

Frequency polygons of the number of scales of two hypothetical species; see discussion in text. Solid line represents species A, broken line represents species B.

If two frequency polygons be constructed to represent graphically the foregoing hypothetical data (Text-fig. 1), the polygons will intersect at a point over the abscissal axis between the points representing 25 and 26

scales. If a vertical line be drawn from the point of intersection of the two polygons, it will be found that 8 specimens of species A cross over to the right of the dividing line, and 6 specimens of species B cross over to the left. The specimens thus crossing over may be said to intergrade. Species A therefore intergrades with respect to species B to the extent of 8%; while species B intergrades with species A in 6% of the individuals. The intergradation is thus not the same in both species. This is a result of the skewness of the frequency distributions and is the usual condition encountered in practice, as stated. However, we want a single figure which will represent the intergradation between two species. This is obtained by taking the simple average of the two figures. The intergradation of species A and B in this hypothetical case is therefore 7%.

We will now take up an actual case and see how this measure works in practice. Let us take the case of *Sciaenops ocellatus*, the northern Atlantic and Gulf coast populations of which diverge sufficiently to place them well up in the following gradated series of examples. The two populations diverge chiefly in the frequency distribution of the number of rays in the second dorsal fin for which the data are given in Table VII, p. 267. These data are



Text-figure 2.

Frequency polygons of the number of articulate rays in the second dorsal fin of two populations of *Sciaenops ocellatus*, based on data given in Table VII, the actual number of specimens being represented. The solid line represents the Chesapeake Bay population; the broken line represents the Texas population. The dotted vertical line represents the dividing line between the two polygons as used throughout the present discussion for the purpose of determining and measuring the degree of intergradation.

represented graphically by Text-fig. 2 which illustrates the frequency polygons of the two populations and the dividing line that forms the basis of determining the measure of intergradation as used throughout the present discussion. Of the northern population 15 specimens cross over to the right of the dividing line, or 14.42% of the composite sample studied comprising 104 specimens; and 50 specimens of the Gulf coast population cross over to the left of the line, or 44.64% of the sample which comprises 112 fish. The simple average of these two percentages, in round figures, is 30, which rep-

resents the measure of intergradation of those two populations. In practice, it is usually not necessary actually to construct the polygons; but the point where the dividing line is to be drawn may be determined by inspection after arranging the data in a frequency distribution table, preferably in the form of percentages (see Table I).

This measure of intergradation, which is uniformly employed in this paper, has the following statistical basis. If the histograms representing the two populations compared be constructed on a percentage basis, the area enclosed by the two overlapping histograms, expressed as a percentage of the sum of their separate areas, equals the measure of intergradation determined as indicated above. In other words, the measure of intergradation as employed for our present purpose represents the measure of the area enclosed by the two overlapping histograms expressed as a percentage. This may be illustrated graphically by the pair of intergrading populations of *Sciaenops ocellatus*.

TABLE I.

Frequency distribution of the number of articulate fin rays in the second dorsal of two races of *Sciaenops ocellatus*, expressed as percentages of the total number of specimens counted of each race, respectively.

Locality	Number of dorsal rays (percentages):					Totals
	22	23	24	25	26	
Chesapeake Bay	3.85	31.73	50.00	13.46	.96	100
Texas coast		6.25	38.39	42.86	12.50	100
The smaller of the overlapping percentages		6.25	38.39	13.46	.96	59.06

Table I gives in percentage form the data represented in Table VII, p. 267. This is necessary for the purpose of constructing the graphs because the number of specimens in the two samples is not the same, the usual condition in practice; whereas, in order to show the normal amount of overlap of the two populations it is necessary to have two samples containing the same number of individuals. Text-figs. 3 and 4 illustrate graphically the data presented in Table I. Text-fig. 3 shows the overlapping histograms of the two populations, the part of each histogram which overlaps the other being distinctively shaded. In Text-fig. 4, drawn to the same scale, the two histograms are shown side by side with the shaded areas the same as in Text-fig. 3. Text-fig. 4 shows at a glance the approximate relation of the sum of the two shaded areas, or the area enclosed by the overlapping histograms, to the sum of the areas of the two histograms. Precisely, this area equals 30%, in round figures, of the sum of the areas of the two histograms. The measure of intergradation is therefore 30% in this particular case. This result may be obtained by adding the smaller of the overlapping frequencies, as shown in Table I, and dividing the sum by 2 in order to get the percentage of the area overlapped to the sum of the two histograms; or by the simple arithmetical calculation as indicated above.

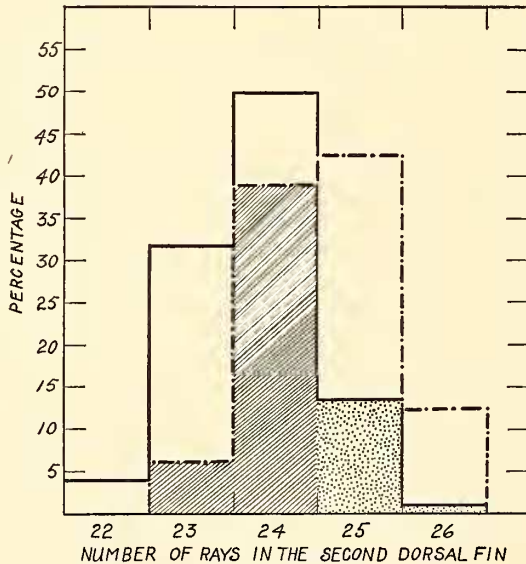
The measure of divergence may be indicated as a percentage also, by subtracting the measure of intergradation as determined above from 100.

The calculation, and hence the number denoting intergradation, or divergence, is always based on the character showing the greatest degree of divergence. There may be some question as to the adequacy of the use of a single character, since we know that populations usually differ in several characters, some of which such as color differences are not readily expressible in definite figures. Some attempts have been made to combine several characters and express the hypothetical sum of their differences by a single fig-

ure. However, I am not at all satisfied that such attempts have succeeded in producing a measure which will more satisfactorily express for our purpose the essential biological facts. Besides, in studying and combining the data for several characters the question will always come up as to just where to draw a line since practically it would be almost impossible to study them all. While not entirely adequate the present measure should prove sufficient for practical purposes, and conclusions arrived at as a result of studies by the standard statistical formulae have been based on a single character. Certainly in the determination of the differences between species or subspecies it is the character which shows the greatest divergence that is the important one to consider. In the method here employed provision is made for taking into consideration other differentiating characters besides the one showing the greatest divergence (see p. 276); although such characters are considered in a general way and not expressed in terms of definite figures. This is probably the best that may be done for the present.

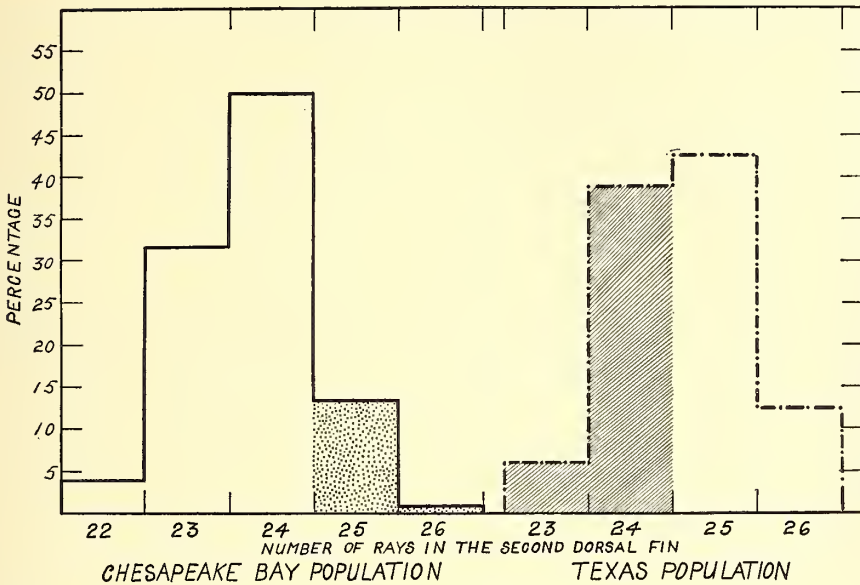
ARITHMETICAL DEFINITION OF SPECIES, SUBSPECIES AND RACE.

Using the above measure, it is proposed tentatively to limit the designation of species and its subdivisions as follows: Other things being equal, a given population is to be considered a race with respect to another closely related population when the average intergradation of the character showing the greatest divergence is between 30% and 40%; a subspecies constitutes a population intergrading between 15% and 25%; it is to be considered a full species when the degree of intergradation is not more than 10%. Con-



Text-figure 3.

Overlapping histograms of the number of articulate rays in the second dorsal fin of two populations of *Sciaenops ocellatus*; based on the same data as Text-figure 2, but the number of specimens in each class expressed as a percentage of the entire sample studied. The solid line represents the Chesapeake Bay population; the broken line represents the Texas population; the hatched space represents the area by which the latter histogram overlaps the former; and the stippled space represents the area by which the former histogram overlaps the latter.



Text-figure 4.

The same two histograms represented in Text-figure 3, separated and placed side by side to give a better picture of the relation of the shaded areas to the sum of the areas of the two histograms. In this particular case the sum of the two shaded areas is 30%, in round figures, of the sum of the areas of the two histograms, and this number represents the measure of intergradation in this particular case. The series of three Text-figures are graphic illustrations showing, by reference to a particular example, how the measure of intergradation as employed for our present purpose, is derived.

comitantly, the divergence between races is 60% to 70%; between subspecies 75% to 85%; and full species diverge to an extent of 90% or more.

For the benefit of those who are used to thinking in terms of graphs the above definition may be paraphrased as follows: When the area enclosed by the two overlapping histograms, constructed on a percentage basis, equals 30 to 40% of the sum of their separate areas, the two populations are to be considered as races; they are considered subspecies when the overlap is 15 to 25%; they are full species when the overlap is 10% or less.

The above proposed boundary lines are discussed on page 275.

THE VARIETY AND FURTHER POSSIBLE SUBDIVISION OF THE SPECIES.

In the above definition of the two principal subdivisions of a species, namely, the subspecies and the race, the maximum intergradation allowed for any population to be included under the latter category is 40%. All pairs of populations which intergrade to a greater extent than 40% are proposed to be grouped under the general category of "variety" and are not further analyzed in our present preliminary study.

In addition to the subdivisions of a species proposed herewith it is evident that the number of such subdivisions may be readily increased by simply narrowing the boundary lines, which are arbitrary anyway, in this completely gradated series. More extensive studies may indicate the de-

sirability of increasing the subdivisions, such as inserting a category between the subspecies and the race, and further subdividing the inclusive category here designated as the variety and consisting of populations which intergrade by more than 40%. The number of categories which may be found desirable to recognize may differ with particular genera or groups. Any such further subdivision should be based not on the rule of the thumb, but on the study and correlation of a sufficient number of actual cases. Most likely in the majority of cases the subdivisions of a species proposed herewith will be found sufficient.

SAMPLING.

The present study would be incomplete without a consideration of the question of sampling. Although I have tried to avoid the use of complex statistical formulae, it will be noted that the present study is largely statistical in its nature. Indeed, if taxonomy is ever to be placed on a high scientific plane it will perforce have to become to a large extent statistical in its methods; although, quite likely, simple statistical deductions will be found sufficient in most cases. One sometimes comes across the statement in taxonomic works that a certain species is a "statistical species," sometimes stated in a rather disparaging manner, as though such a species is not of much account. However, probably the majority of closely related species of fishes are "statistical species." The reason taxonomists were able to make this distinction between "statistical species" and those supposedly not statistical, is because their studies were largely based on but a few specimens, as noted above (p. 255). A "statistical species" is simply one which diverges from a closely related species to a comparatively low degree so that even the study of a few specimens shows the close approach or even intergradation of the frequency distributions of the differentiating characters.

The importance of proper sampling in statistical studies in general is universally appreciated, and it is not necessary to consider the subject here at any length. It will be sufficient here to state that, except in a few cases such as the complete enumeration of the population of a country during a census, the description of certain attributes of a population is in reality a description of the attributes of the sample which has been studied, and the value of the description is dependent on how nearly the sample is representative of the population as a whole.

The same is true of the description of species, subspecies, races or varieties. If a species is described from a single specimen or from a few specimens, the account in reality represents a description of those specimens. While in many cases such a description is sufficient for practical purposes to identify and distinguish the species, in many other cases such an account will be found entirely inadequate. Related species may be so close that it takes the detailed study of many specimens to establish their divergence. In such cases proper sampling becomes of importance; although in the case of populations which reach a sufficiently high degree of divergence to be regarded as full species, sampling is not of as transcendent importance as in populations showing a relatively higher degree of intergradation.

In my own studies during which the data presented below were obtained, I was impressed time and again with the importance of proper sampling. It was noted frequently that specimens in the same lot bearing the same data, evidently having been obtained in one or but a few drags of the net in the same place at the same time, and consequently, most likely having a common, immediate genotypic origin, would tend to group themselves, in a predominant manner, within a narrowly circumscribed space, sometimes even near either end of the frequency distribution of their species or race as a whole. This was noted especially in cases where the specimens in the lot were

of nearly the same size. Consequently, it may be readily appreciated that if the sample studied be obtained in one, or but a few drags of the net made at the same time in the same place, it is quite likely that it would not give a true picture of the population in many cases.

In obtaining the data presented below due attention was paid to the question of sampling. As stated above, the data were obtained incidentally in the course of taxonomic studies of the fishes. They were taken from lots of specimens obtained at different times by various collectors. In no case was a definite plan of sampling the particular population devised and carried out. Under the circumstances, the method of sampling which I adopted was as follows.

For the sake of brevity and clarity it is proposed to designate all the specimens from which the final data in a Table are drawn, as the *composite sample* and the smaller samples which go to make up the composite sample, as *constituent samples*. It has been stated that if the composite sample is obtained in one drag of the net, that is, it has but one constituent sample, it will quite likely not give a true picture of the population. The greater the number of constituent samples the more nearly will the data approach the true distribution of the population as a whole. As a consequence of these premises, it was my aim to include as many constituent samples as it was possible to obtain from the available material. If, for instance, I had 25 containers of specimens representing as many lots of fish taken on different dates, in different places, and 20 containers had but 1, 2, or 3 specimens each, while the other 5 containers had much larger numbers, the 20 smaller lots were included in the study, and only part of the specimens of each of the larger lots. Of course, my sampling was limited by the material available, but in every case I tried to come as near to my aim as was possible. The number of constituent samples will be stated hereafter under each example cited, so that the reader may judge as to the adequacy of the sampling. (For the meaning of the notation adopted see footnote on p. 264). I am confident that in most cases at least the given distributions represented by the composite samples are more or less fairly representative of their populations for practical purposes.

In some cases the number of specimens studied were too few to constitute a satisfactory composite sample, such as in case of the two races of *Hippocampus zosterae*, in *H. punctulatus*,² and in *Gobiosoma boscii* and *G. robustum*. Since it is my hope that the method adopted herein will serve as a useful guide for taxonomists who frequently and of necessity have to work with quite small samples, these examples are included in our series. Further remarks regarding sampling in the above three cases are given under their accounts.

EXAMPLES OF VARIETIES.

Cynoscion regalis. This species is discussed below in another connection and the frequency distributions of the number of dorsal rays are given in Table IX, p. 269. Turning to that Table and comparing the population of Chesapeake Bay with that from the east coast of Florida, it will be noted that the dividing line to be drawn according to the simple method outlined above, is between the columns representing 27 and 28 rays. Of the Chesapeake Bay population 21 specimens of a total of 40, or 52.50% of the composite sample, cross over to the left of the dividing line. The percentage of intergradation of the Chesapeake Bay population as compared with that of Florida is therefore 52.50. Likewise, of the Florida population

² The notation for subspecies employed in this paper is in accordance with the suggestion made on p. 284.

43 specimens out of a composite sample of 110, cross over to the right of the dividing line, representing an intergradation of 39.09%. The simple average of these two intergradations, 46 in round figures, represents our measure of intergradation. The measure of divergence in this case is 100 minus 46, or 54%. Constitution of composite samples: Chesapeake Bay 1 (4)³, 2 (4), 7 (1), 8 (1), 13 (1); Florida 5 (1), 28 (1), 77 (1). The two larger constituent samples from Florida do not bear any more definite data than the locality and month and each one possibly contains more than one constituent.

Cynoscion nebulosus. The well known spotted sea trout of the southern states is a common food and game fish from Chesapeake Bay to Texas, ranging northward, in diminishing numbers, to New York. For an account of the species the reader may be referred to any general work dealing with the fishes of the region where it occurs, such as the "Fishes of Chesapeake Bay" by Hildebrand and Schroeder (1928). No extensive study has been made as yet of its racial differentiation; but there is found a statistically measurable difference in the number of dorsal fin rays in fish from the Gulf coast as compared with those from Chesapeake Bay on the Atlantic Coast. It is possible that a more extensive study will reveal other characters showing a greater degree of divergence, but this is quite doubtful. At any rate, the dorsal fin ray count evidently shows sufficient divergence to be useful as an illustration in the present study.

TABLE II.

Frequency distribution of the number of articulate rays in the second dorsal of *Cynoscion nebulosus*.

Locality	Number of rays in second dorsal				
	23	24	25	26	27
Chesapeake Bay	1	17	53	31	6
Texas coast	1	12	38	48	5

The dividing line in this case is drawn between the columns representing 25 and 26 rays. The Texas population intergrades by 49.04%, while the Chesapeake Bay population intergrades 34.26%. The average intergradation in this case is 42% and the divergence 58%. Constitution of composite samples: Chesapeake Bay 1 (15), 2 (3), 3 (2), 5 (2), 6 (2), 16 (1), 43 (1); Texas 1 (2), 2 (4), 3 (2), 4 (2), 5 (3), 6 (1), 7 (2), 10 (1), 17 (1), 18 (1).

Although this example does not form a happy choice for the purpose of illustration, it is included in our series because similar cases no doubt will be encountered in practice. It will be noted that if the polygons representing the above data be constructed they will overlap at three points. Consequently, our method of drawing the dividing line and calculating the intergradation

³ For the sake of brevity the sampling of every case cited in this paper is indicated by figures which have the following meaning. As suggested above (p. 263), the entire number of specimens of a given population, on which the final distribution in any one Table is based, is designated as the composite sample, while each lot of specimens bearing the same data is known as a constituent sample, a variable number of constituents going to make up the composite sample, depending on the particular population used as an example. In the notation adopted a figure outside a parenthesis indicates the number of specimens in one or more constituent samples, while a figure within a parenthesis gives the number of constituent samples each one of which contained the number of specimens indicated by the preceding figure. Thus, the composite sample of *C. regalis* from Chesapeake Bay was made up of 11 constituent samples, four of which had 1 specimen each, four constituents had 2 specimens each, while the remaining three had 7, 8 and 13 specimens, respectively.

does not apply strictly to the present case. However, it will be noted also that if one specimen from the Texas population be dropped at one extreme end and two specimens from the Chesapeake Bay population be dropped at the other end, the two polygons will overlap at one point as usual. This small irregularity caused by one and two specimens out of a little over a hundred in either composite sample, very likely is caused by the imperfection of sampling, and any such irregularity at either extreme where the number of specimens are few, is not likely to be compensated readily. At any rate, whatever the cause, for the purpose of computing the degree of intergradation by our present method, this small irregularity is disregarded. It is to be noted that computing by the standard formula (see Table XVII) the degree of difference between these two distributions almost reaches a "significant" figure.

EXAMPLES OF RACES.

Bairdiella chrysura. This is a very common fish on the east coast of the United States. A recent and quite extensive account of the life history of the species has been published by Hildebrand and Cable (1930). Like the preceding species its races have not been studied extensively as yet, but there is a difference in the frequency distributions of the dorsal fin rays between southern and northern fish, as follows.

TABLE III.

Frequency distribution of the number of articulate rays in the second dorsal of *Bairdiella chrysura*.

Locality	Number of rays in second dorsal				
	19	20	21	22	23
Chesapeake Bay	2	11	26	28	3
Texas coast	3	19	37	12	

If a line be drawn between the columns representing 21 and 22 rays, it will be found that the Chesapeake Bay population intergrades with that of the Texas coast to the extent of 55.71%, while the Texas population intergrades 16.9%, giving an average intergradation of 36% and a divergence of 64%. Sampling: Chesapeake Bay 1 (14), 2 (8), 3 (6), 4 (3), 5 (2); Texas 1 (6), 2 (1), 4 (2), 5 (1), 6 (1), 19 (1), 25 (1).

Fundulus confluentus. This is a rather common, small, cyprinodont fish originally described from Lake Monroe, Florida, by Goode and Bean (in Goode 1879, p. 118). The original description is in error in some important details, and the species has been confused with related species by all later authors which I consulted. However, it is a well marked species which may be distinguished without undue difficulty from its congeners occurring with it through a greater part of its range. An account of the species will be included in a revision of the genus which is under preparation. The Chesapeake Bay population of this species differs racially from that of Florida. In addition to a rather slight and variable difference in the color pattern, the structural character showing the greatest divergence is found in the number of rays in the anal fin as follows.

TABLE IV.

Frequency distribution of the number of anal rays in *Fundulus confluentus*.

Locality	Anal rays		
	9	10	11
Norfolk, Va.	23	35	
Beaufort, N. C.		19	1
Florida	2	21	2

It will be noted that the Chesapeake Bay population tends to have a markedly lower anal fin ray count. The population from North Carolina nearly agrees with that of Florida in the number of fin rays, but the color pattern is more nearly like that of the Chesapeake Bay population. Drawing the dividing line between the columns representing 9 and 10 rays and comparing the Chesapeake Bay population with that of Florida, it will be found that the former population intergrades by 60.34% and the latter by 8%; or an average intergradation of 34%. Sampling: Norfolk 3 (1), 9 (1), 14 (1), 32 (1); Florida 1 (6), 2 (1), 5 (1), 12 (1). This is the only example, of all those cited here, in which the well marked modes of both populations fall on the same side of the dividing line.

Hippocampus zosterae. In reviewing the species of its genus found in American waters I (1937) studied material of this species from Pensacola, Captiva Pass and Key West, and the data presented herewith are taken from my paper, where the question of racial differentiation is taken up in greater detail. The populations from the three localities differ, on the average, in the number of trunk segments and the number of rays in the pectoral fin, the former character showing the greatest divergence as follows.

TABLE V.

Frequency distribution of the number of trunk segments of *Hippocampus zosterae*.

Locality	Trunk segments		
	9	10	11
Key West ⁴	4	16	1
Captiva Pass	5	12	1
Pensacola ⁵	7	6	

It is to be noted that the greatest divergence exists between the Pensacola and Key West populations, while the Captiva Pass population is somewhat intermediate but nearer to that of Key West. This gradual differentiation with latitude is a frequently recurring phenomenon which is well known to students of fishes. In a case of this kind and in the absence of a more elaborate study of the species, we may compare the extremes. If a line be drawn between the columns representing 9 and 10 segments, it will be found that the Key West population intergrades with that from Pensacola to the extent of 19.05%, while the latter intergrades with the former by 46.15%, giving an average intergradation of 33%. Sampling: Pensacola 1 (2), 11 (1); Key West 1 (6), 2 (1), 3 (1), 4 (1), 6 (1).

⁴ Including 4 specimens from Newfound Harbor.

⁵ Including 1 specimen from Apalachicola.

The available material of this species is not sufficient to constitute a satisfactory sample; but the difference between the populations is significant, especially when considered in connection with the small spread of the frequency distribution, and approximately this difference very likely will be found to exist after a more satisfactory sampling (see also remarks on p. 263).

Leiostomus xanthurus. This species is the well known spot, a common market fish on the east coast of the United States. The most comprehensive account of its life history published so far is that by Hildebrand and Cable (1930). Almost nothing is known now regarding the racial differentiation of the species; but I found a significant difference in the number of rays in the second dorsal on comparing fish from Chesapeake Bay with those from the coast of Texas, as follows.

TABLE VI.

Frequency distribution of the number of articulate rays in the second dorsal of *Leiostomus xanthurus*.

Locality	Number of rays in second dorsal					
	28	29	30	31	32	33
Chesapeake Bay		5	25	33	18	
Texas coast	1	25	50	20	6	1

The dividing line is drawn between the columns representing 30 and 31 rays. The Chesapeake Bay population intergrades 37.04% and that of the Texas coast 26.21% giving an average intergradation of 32%. Sampling: Chesapeake Bay 1 (3), 2 (2), 3 (5), 4 (1), 5 (1), 10 (1), 20 (2); Texas 1 (5), 2 (2), 3 (1), 4 (1), 5 (1), 6 (1), 17 (1), 19 (1), 20 (2).

Sciaenops ocellatus. This species is the well known redfish in the markets of the Gulf coast, the celebrated channel bass of sportsmen. For an account of the species the reader may again be referred to Hildebrand and Schroeder (1928). The racial differentiation of this species likewise has not been studied to any extent, but there is a significant difference in the number of rays in the second dorsal when the Chesapeake Bay population is compared with that of the Gulf coast as follows.

TABLE VII.

Frequency distribution of the number of articulate rays in the second dorsal of *Sciaenops ocellatus*.

Locality	Number of rays in second dorsal				
	22	23	24	25	26
Chesapeake Bay	4	33	52	14	1
Texas coast		7	43	48	14

The dividing line in this case is drawn between the columns representing 24 and 25 rays. The intergradation of the Texas coast population is 44.64%, that of the Chesapeake Bay population 14.42%, or an average intergradation of 30%. Sampling: Chesapeake Bay 1 (1), 2 (1), 3 (1), 5 (1),

6 (1), 22 (1), 28 (1), 37 (1); Texas 1 (5), 2 (1), 4 (2), 5 (1), 8 (1), 10 (1), 12 (2), 21 (1), 29 (1).

EXAMPLES OF SUBSPECIES.

*Hippocampus punctulatus*₂ and *H. hudsonius*₂. These seahorses from the east coast of the United States and the coast of Cuba have been generally recognized as independent species by American ichthyologists. However, they have been badly confused, and their structural characters have been stated incorrectly in most current accounts. A discussion of their morphological and geographical limits is given in my review of the species of *Hippocampus* (1937) where it is determined that the character showing the greatest divergence between them is found in the number of caudal segments, as follows.

TABLE VIII.

Frequency distributions of the numbers of caudal segments of *Hippocampus hudsonius*₂ and *H. punctulatus*₂.

Locality and subspecies	Number of caudal segments						
	33	34	35	36	37	38	39
<i>H. hudsonius</i> ₂							
Chesapeake Bay to Maine			3	7	15	7	4
North and South Carolina			1	7	8	1	
Mississippi to Texas			1	5	10	2	
<i>H. punctulatus</i> ₂							
Florida and Cuba	1		8	10	7		

As in *H. zosterae* (see p. 266), the greatest divergence is found between the northern population, Chesapeake Bay to Maine, and the southern, Florida and Cuba. The population from the Carolinas and that from Mississippi to Texas are somewhat intermediate but nearer to the northern population. Other characters as well gradually differ with latitude. Although there is a gradual change in morphology with latitude, it nevertheless seems desirable to recognize two subspecies as discussed on page 277.

In this case the dividing line is drawn between the columns representing 36 and 37 caudal segments. Comparing the extreme northern population of *hudsonius*₂ with the extreme southern population, *punctulatus*₂, the former intergrades the latter by 27.78%, and the latter intergrades the former by 26.92%, or an average intergradation of 27%. Also, in order to show the normal morphological range of *hudsonius*₂ as a whole, the data from North and South Carolina and Mississippi to Texas are combined with those from Chesapeake Bay and northward. Combining the data as indicated, the northern *H. hudsonius*₂, intergrades with the southern *H. punctulatus*₂, to the extent of 33.80%, while the latter intergrades by 26.92%, giving an average intergradation of 30%. The composite sample of *H. hudsonius*₂ consists of 54 constituent samples as follows: 1 (43), 2 (7), 3 (3), 5 (1). Some of the constituents having more than one fish do not have the data any more specific than the name of the state on the coast of which they were captured, and they quite likely represent more than one constituent. At any rate, the number of constituents in the composite sample is not less than 54. The composite sample of *H. punctulatus*₂ consists of 23 constituent samples, as follows: 1 (21), 2 (1), 3 (1). The specimens in the composite sample of

*punctulatus*₂, are very few, but they represent the limit of my available material. While lacking in numbers it consists of many constituents and possibly fairly represents its population (see also remarks on p. 263).

*Cynoscion arenarius*₂ and *C. regalis*₂. The differences between these two common subspecies from the east coast of the United States have been discussed by me (1929) and the reader is referred to that paper for details. In grown specimens the character showing the greatest divergence seems to be found in the number of gill rakers on the outer gill arch; while the number of dorsal rays shows the next greatest divergence. However, the number of gill rakers is not susceptible of precise determination for reasons stated in the paper cited. Should it be found possible to discount the difficulties inherent in a precise determination of that character, it is doubtful whether it would prove to show greater divergence than the number of dorsal rays. On the other hand, the latter character is susceptible of absolutely precise determination at all stages of growth, soon after the fin rays have developed in the young fry. For the purpose of the present discussion it may be assumed that that character shows the greatest divergence.

TABLE IX.

Frequency distribution of the number of articulate dorsal rays in *Cynoscion regalis*₂ and *C. arenarius*₂.

Locality and subspecies	Number of dorsal rays					
	24	25	26	27	28	29
<i>C. regalis</i> ₂						
Chesapeake Bay		1	5	15	16	3
North and South Carolina		1	6	21	12	
Cape Canaveral and Fernandina, Fla.		3	15	49	35	8
<i>C. arenarius</i> ₂						
Louisiana and Texas	2	35	59	22	1	

The dividing line in this case falls between 26 and 27 rays; *C. arenarius*₂ intergrading 19.33% and *C. regalis*₂ 16.32%, resulting in an average intergradation of 18%. The sampling of the populations of *regalis*₂ from Chesapeake Bay and from the coast of Florida has been indicated above (p. 264); while that from the Carolinas is as follows: 3 (2), 4 (1), 7 (1), 8 (1), 15 (1). Of *arenarius*₂ 69 specimens do not have any specific data by which the number of constituent samples could be determined; the rest consists of 14 constituents as follows: 1 (9), 2 (1), 5 (1), 6 (2), 22 (1).

EXAMPLES OF SPECIES.

Hippocampus regulus and *H. zosterae*. The former species is closely related to the latter, the races of which have been discussed above. More extensive accounts of the two species and a discussion of their relationship are given in my (1937) review. It will be sufficient to state here that besides its somewhat smaller size, and a slightly greater average number of trunk segments, *H. regulus* differs chiefly from *H. zosterae* in having a smaller number of caudal segments and fewer dorsal rays, the greatest divergence occurring in the latter character, as follows:

TABLE X.

Frequency distribution of the number of dorsal rays in *Hippocampus regulus* and *H. zosterae*.

Locality and species	Number of dorsal rays				
	10	11	12	13	14
<i>H. regulus</i>					
Mississippi and Texas	2	15	1		
Campeche, Mexico		5			
<i>H. zosterae</i>					
Key West, Fla. ⁶		4	13	5	
Captiva Pass, Fla.			16	2	
Pensacola, Fla. ⁷		2	9		1

An inspection of the foregoing Table shows that this character tends to be fairly constant within the limits of each species, there being no pronounced racial divergence as was found above for the number of trunk segments of *H. zosterae*. The Key West population shows a tendency to have a slightly smaller average—thus surprisingly more nearly approaching *regulus* from Mississippi and Texas than the Pensacola race of *zosterae* approaches *regulus*—but the difference is slight. The divergence of the two species in this case is measured by drawing a dividing line between the columns representing 11 and 12 rays. *H. zosterae* is thus found to intergrade to the extent of 11.54%; *H. regulus* intergrades 4.35%; giving an average intergradation of 8%. Sampling: *H. regulus* 1 (3), 2 (5), 5 (2); *H. zosterae* 1 (7), 2 (2), 3 (2), 6 (1), 11 (1), 18 (1).

Gobionellus boleosoma and *G. shufeldti*. Accounts of these two species of gobies and a discussion of their relationship will be found in my (1932) revision of the genus. Briefly, the two species differ in the maximum size to which they attain, in their color pattern, in the relative length of the ventral fin, in the extent of squamation in front of the dorsal, and in the number of dorsal and anal rays. However, none of these differences is absolutely decisive when each one is considered by itself, and individual fish often can not be distinguished and identified with assurance by any one single character, although there is usually no trouble in referring individual fish to their proper species when all the differentiating characters are taken in consideration. The greatest divergence between the two species is shown by the number of anal rays, as follows.

TABLE XI.

Frequency distribution of the number of anal rays in *Gobionellus boleosoma* and *G. shufeldti*.

Species	Number of anal rays			
	11	12	13	14
<i>G. boleosoma</i>	3	74	4	
<i>G. shufeldti</i>		3	33	1

⁶ Including 3 specimens from Newfound Harbor and 2 from Biscayne Bay.

⁷ Including 1 specimen from Apalachicola.

The dividing line in this case is between 12 and 13; the intergradation calculated for *G. shufeldti* is 8.11%, and for *G. boleosoma* 4.94%, resulting in an average intergradation of 7%. The counts of the fin rays in these two species are fairly constant throughout their ranges, there being no pronounced racial differences in this respect. Sampling: *G. boleosoma* 1 (13), 2 (8), 3 (1), 4 (1), 6 (1), 39 (1); *G. shufeldti* 1 (2), 8 (1), 13 (1), 14 (1).

Paralichthys lethostigma and *P. albigutta*. Some recent investigators have expressed doubt in regard to the distinctness of these two common species of flounders. This doubt is apparently caused by the fact that the chief differentiating characters are of a meristic nature, that is, quantitative, and vary within rather wide limits. Consequently, when specimens near the beginning or near the end of the two frequency distributions of the two species, respectively, are encountered, they may be referred to either species when any single character is considered. However, after preparing tables for the several characters showing the normal frequency distributions of each species, it becomes an easy matter, with the aid of such tables, to refer individual fish to their proper species. An extensive discussion of the differences between these two species, among others, is included in a revision of the genus which I now have completed in manuscript form. In connection with that study, I examined over 500 specimens representing both species, and out of this large number I encountered only one specimen the status of which was in doubt. Besides the structural differences the two species differ also in their color pattern. Without going here into details, it may be stated that the least intergradation is found in the number of anal rays, as follows.

TABLE XII.

Frequency distribution of the number of rays in the anal fin of *Paralichthys albigutta* and *P. lethostigma*.

SPECIES	NUMBER OF RAYS IN ANAL FIN																								
	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77
<i>P. albigutta</i>	1	1	4	10	15	16	26	17	11	5	5														
<i>P. lethostigma</i>											2	5	10	15	25	27	31	13	14	9	1				1

Drawing the dividing line between 63 and 64 rays, it is found that *P. lethostigma* intergrades 1.31%; but no specimens of *P. albigutta* cross over to the left of the line, the intergradation of the latter thus being 0. The average intergradation is then 1% in round numbers. The composite sample of *P. albigutta* includes 70 specimens from the vicinity of Beaufort, N. C., and 16 from the vicinity of Corpus Christi, Texas, for which no detailed data are available, probably containing a number of constituents. The rest are from the Gulf of Mexico, except two specimens from the Atlantic coast, and altogether consist of 16 constituents as follows: 1 (9), 2 (6), 4 (1). The composite sample of *P. lethostigma* contains 13 specimens from Beaufort, N. C., without any further data, but probably obtained on different dates; 7 other specimens from the Atlantic coast and 133 from the Gulf coast. The sampling of all except the 13 is as follows: 1 (11), 2 (4), 3 (2), 4 (3), 5 (1), 6 (1), 7 (1), 8 (1), 9 (1), 10 (1), 12 (2), 13 (1), 21 (1).

Gobiosoma bosci and *G. robustum*. An extensive discussion of the relationship between these two species of gobies was published in my (1933) revision of the genus. Besides a difference in the color pattern which, however, is not always distinctive, the chief structural characters differentiating the two species are: the number of dorsal and anal rays and the length of the ventral. The numbers of fin rays intergrade in the two species; but the length of the ventral expressed as the number of times it enters into the distance between the ventral and anal origins, does not show any intergradation in the specimens measured, as follows.

TABLE XIII.

Frequency distribution of the length of the ventral in *Gobiosoma bosci* and *G. robustum*, expressed as the numerical value of the ratio of the distance from base of ventral to origin of anal, to the length of the ventral.

Species	Length of ventral in the distance from its base to origin of anal								
	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0
<i>G. bosci</i>					2	4	8	2	1
<i>G. robustum</i>	3	7	2	4					

In this case then intergradation is zero and divergence 100%. The heading numbers for the classes in the above table represent the mid-values, this example being an illustration of a character the measurements of which form a continuous series. Sampling: *G. bosci* 1 (9), 2 (4); *G. robustum* 1 (5), 2 (1), 4 (1), 5 (1). The composite samples are entirely inadequate but there is no question in regard to the specific distinctness of the populations compared (see also remarks on p. 263).

It should be stated also that the chief differentiating character which distinguishes these two species is not susceptible of determination with a high degree of accuracy. Although proportional measurements are widely employed for separating closely related populations of fishes, of specific or lower rank, such measurements can be determined only by a rather rough approximation to their true value. The values of the measurements, more likely than not, are apt to vary with the state and method of preservation of the specimens and also with the observer making the measurements. Even the same observer measuring the same specimens with the same instruments is apt to obtain somewhat different results by successive trials; although when sufficient care is exercised and a vernier caliper employed for taking the measurements, the results usually are sufficiently accurate for practical purposes even in the case of quite small specimens. Anyway, since the data represented in the above Table are not entirely satisfactory we may cite the following case which occupies the same position in our series, and which is based on a character that is susceptible of being determined with almost absolute accuracy.

Lepidogobius y-cauda and *L. guaymasiae*. These two gobies were described originally by Jenkins and Evermann (1888) from the Gulf of California. The two species are very closely related, and all later authors considered the above two names as synonymous. Indeed, the original descriptions are not sufficient to distinguish the two species, are erroneous in some important details, and it is very doubtful whether even the original describers separated all of their material properly. Nevertheless, the two

species are quite distinct. The differences distinguishing these two species will be taken up in greater detail in a revision of their genus which is now in process of preparation. It will suffice for our present purpose to state that the greatest divergence is shown by the number of pectoral rays as follows.

TABLE XIV.

Frequency distribution of the number of pectoral rays in *Lepidogobius y-cauda* and *L. guaymasiae*.

Species	Number of pectoral rays							
	20	21	22	23	24	25	26	27
<i>L. y-cauda</i>	6	23	11					
<i>L. guaymasiae</i>				7	51	42	5	1

In this case also intergradation is zero and divergence 100%, as far as the samples studied are concerned. Sampling: *G. y-cauda* 1 (1), 2 (2), 5 (1), 6 (1), 24 (1); *G. guaymasiae* 2 (2), 14 (1), 34 (1), 54 (1).

Paralichthys dentatus and *P. lethostigma*. The latter species was compared above with *P. albigutta*, with which it showed a slight amount of intergradation. When compared with another species of its genus, with *dentatus*, it does not show any intergradation. *P. dentatus* has a more northern distribution. It is the well-known summer flounder or fluke and is an important commercial species. Its range extends from Cape Cod to northern Florida. On the coast of North Carolina and southward its geographical range overlaps with its two common congeners which were discussed above. An extensive account of this species is included in my manuscript referred to above. For a published account of the species the reader is referred to "Fishes of Chesapeake Bay" by Hildebrand and Schroeder (1928), this being the only species of *Paralichthys* occurring in that body of water. For the purpose of the present discussion it may be stated that *P. dentatus* has nearly the same frequency distribution of the number of fin rays as *P. lethostigma*, but it differs decidedly in the number of gill rakers, as follows.

TABLE XV.

Frequency distribution of the number of gill rakers on the lower limb of the first gill arch of *Paralichthys dentatus* and *P. lethostigma*.

Species	Number of gill rakers on lower limb										
	8	9	10	11	12	13	14	15	16	17	18
<i>P. lethostigma</i>	7	67	66	6							
<i>P. dentatus</i>						4	3	18	44	35	11

The foregoing is an illustration of a case where a gap exists between two species with reference to a given character. The composite sample of *lethostigma* consists of 24 specimens from localities ranging from Albemarle Sound, N. C., to St. John's River, Florida, on the Atlantic coast, and 122 from the coasts of Texas and Louisiana (including 1 specimen from Apalachicola, Fla.). The Atlantic coast specimens include 13 from Beaufort, N. C., without any more detailed data, probably a mixed lot, and 7 other constituents as follows: 1 (3), 2 (4). The composite sample from the

TABLE XVI.
Summary of the preceding data showing the gradual continuity of intergradation and divergence arranged in order of decreasing intergradation, or increasing divergence.

Population showing greatest degree of intergradation	As compared with	Family	Percentage intergradation of first population	Percentage intergradation of 2nd population	Measure of intergradation	Measure of divergence	$\frac{sM_1 - M_2}{\sqrt{E_1^2 + E_2^2}}$	Taxonomic rank of the population
<i>Cynoscion regalis</i> Chesapeake Bay	<i>C. regalis</i> Florida Coast	Sciaenidae	52.50	39.09	46	54	.9	variety
<i>Cynoscion nebulosus</i> Texas coast	<i>C. nebulosus</i> Chesapeake Bay	"	49.04	34.26	42	58	2.7	"
<i>Bairdiella chrysura</i> Chesapeake Bay	<i>B. chrysura</i> Texas coast	"	55.71	16.90	36	64	4.9	race
<i>Fundulus confluentus</i> Chesapeake Bay	<i>F. confluentus</i> Florida	Cyprinodontidae	60.34	8.00	34	66	5.7	"
<i>Hippocampus zosterae</i> Pensacola	<i>H. zosterae</i> Key West	Syngnathidae	46.15	19.05	33	67	3.4	"
<i>Leiostomus xanthurus</i> Chesapeake Bay	<i>L. xanthurus</i> Texas coast	Sciaenidae	37.04	26.21	32	68	8.2	"
<i>Sciaenops ocellatus</i> Texas coast	<i>S. ocellatus</i> Chesapeake Bay	"	44.64	14.42	30 ^o	70	12.0	"
<i>Hippocampus hudsonius</i> ₂ North of Florida	<i>H. punctulatus</i> ₂ Florida and Cuba	Syngnathidae	33.80	26.92	30 ^o	70	6.8	subspecies
<i>Cynoscion arenarius</i> ₂ Gulf coast	<i>C. regalis</i> ₂ Atlantic coast	Sciaenidae	19.33	16.32	18	82	22.1	"
<i>Hippocampus zosterae</i>	<i>H. regalis</i>	Syngnathidae	11.54	4.35	8	92	15.0	species
<i>Gobionellus shufeldti</i>	<i>G. boleosoma</i>	Gobiidae	8.11	4.94	7	93	22.1	"
<i>Paralichthys lethostigma</i>	<i>P. albivitta</i>	Pleuronectidae	1.31	0	1	99	53.0	"
<i>Gobiosoma robustum</i>	<i>G. boscii</i>	Gobiidae	0	0	0	100	17.8	"
<i>Lepidogobius y-cauda</i>	<i>L. guaymasiae</i>	"	0	0	0	100	40.0	"
<i>Paralichthys lethostigma</i>	<i>P. dentatus</i>	Pleuronectidae			minus	gap	85.1	"

Gulf coast is constituted as follows: 1 (6), 2 (4), 3 (4), 5 (1), 6 (1), 8 (1), 9 (1), 10 (1), 12 (2), 13 (1), 21 (1). The composite sample of *P. dentatus* consists of 71 specimens from Chesapeake Bay constituted as follows: 1 (28), 2 (8), 3 (5), 5 (1), 7 (1); 37 specimens from Beaufort, N. C., for which no further data are available, probably a mixed lot; 7 specimens comprising 6 constituent samples from North Carolina to Georgia.

RECAPITULATION.

The data presented above of a series of actual cases in widely dissimilar groups of fishes, arranged to show the degree of divergence in a gradually ascending series, are recapitulated in tabular form on page 274, in order to give a birdseye view of the gradual continuity of the series. Table XVI shows the gradualness of divergence or intergradation and that any line drawn between the species concept and its subdivisions must be arbitrary. The continuity of the series is not as gradual as may be desired. A more evenly gradual continuity will no doubt be obtained by studying and citing a greater number of examples. However, those cited seem sufficient for this preliminary study to establish in a definite manner the gradualness of divergence in nature. Beside their number, the kinds of examples cited are not as well chosen as I would have liked them to be. I have now under study other populations which show promise of furnishing better proof to clinch the present thesis. However, the differentiation of those populations has not been satisfactorily established as yet, and the accumulated data are not of sufficient extent to enable me to use those data with assurance. While the examples cited are sufficient to prove the proposition in this preliminary paper, the subject evidently can not be expected to be exhausted in a single article.

THE ARBITRARY BOUNDARIES BETWEEN SPECIES, SUBSPECIES AND RACE.

The propriety and expediency of the arbitrary boundaries between the three main taxonomic units proposed in this paper may now be considered after having determined just how intergradation occurs in nature.

It may be suggested by a study of Table XVI that a more logical boundary to draw between the species and subspecies would be between two other pairs of population, namely, *Paralichthys lethostigma* and *P. albigutta*, and *Gobiosoma boscii* and *G. robustum*. That is, two populations are to be regarded as fully distinct species only when they differ in any single character in such a manner that there is no intergradation between them. However, this suggestion can be defended neither on theoretical nor on practical grounds.

First of all it may be stated that there is nothing of an inherently fundamental nature in such a boundary line. In a gradually continuous series such as we are dealing with, it is just as arbitrary as any other dividing line which may be proposed. Even when a gap exists between two species it may be possible to devise such a measure as will express the degree of the extent of the gap and the series denoting divergence continued in a gradual manner, although for our present purpose it is not deemed necessary to devise such a measure.

FOOTNOTES TO TABLE XVI.

⁸ This column is added for the purpose of comparing the method here employed with the standard method, as discussed on page 279. However, this does not form an essential part of our method, and the column as well as the discussion may be left out of consideration by those readers who are not interested in making this comparison.

⁹ The sampling of the pairs of populations of *S. ocellatus* and *H. hudsonius* is not altogether comparable as discussed on page 277. When the extreme populations of the latter species are compared the intergradation is 27%.

Second, it should be remembered that two diverging populations, especially when they reach such a high degree of divergence as to constitute species or subspecies, usually differ in several characters. Sometimes a high degree of divergence may be shown by two or more characters, although no single character may show a divergence of 100%. In such cases individual specimens may be referred with comparative ease to their proper species by at least one of these characters falling decidedly near the mode of its species. (This point is taken up more fully in my manuscript study of the genus *Paralichthys*). It is evident, therefore, that the boundary line under discussion can not be defended on theoretical grounds.

On practical grounds also such a boundary line will not prove satisfactory. If this boundary is adopted, possibly the majority or at least a large percentage of closely related species of fishes now universally recognized will have to be reduced to subspecific rank because of the general or at least frequent existence of intergrades. A case in point is the difference between *Gobionellus boleosoma* and *G. shufeldti* which forms one of the preceding illustrations. Probably no taxonomist who would compare and study authentic specimens of these two species would do otherwise but come to the conclusion that they represent fully distinct and independent species. In fact the differences between them are more numerous and saliently marked than in many other species which are now generally recognized. In spite of all this, their chief differentiating character intergrades in 8% of the individuals of *G. shufeldti*, or 7% as an average between the two.

It is evident, therefore, that a boundary line drawn so that two populations in which the average intergradation of the most divergent character is 7% or less are considered fully distinct, is not far fetched. The figure proposed herein, 10%, is not based on sufficient definite data, but is chosen chiefly for the simple reason that it represents a conveniently round number in our decimal system. Since such a boundary line is arbitrary anyway, the one proposed here tentatively is sufficient for the purpose of discussion. It is evident that the boundary line will be drawn the more advantageously in accordance with the facts of nature, the greater the number of cases which are studied in detail and correlated, and quite likely will change with increased knowledge. It may also be found advantageous to fix different boundaries in special cases or in certain groups in order to give in such cases an interpretation of the facts which will more closely approach nature.

The proposed boundary between the subspecies and the race also seems the most expedient as judged by the evidence considered.

In the arithmetical definition of species, subspecies and race given on page 260, it is to be noted that gaps are left in the continuity of the percentages at the boundary lines between the species and subspecies on the one hand and the subspecies and the race on the other. This is done on purpose. Also, the phrase "other things being equal" is used advisedly. As a matter of fact, other things usually are not equal. Populations, especially those that reach a sufficiently high degree of divergence to be regarded properly as species or subspecies, usually differ in many characters, the nature, number and variability of which vary widely with the particular populations, and all the characters have to be taken in consideration. Since any single character does not absolutely determine the taxonomic status of a population, it is evident that in appraising the sum total of values of the other characters in which two populations differ, there will be room for difference of opinion in cases where the difference between the two populations falls *near* any arbitrary lines which may be fixed. This is as it should be. The very nature of the subject matter excludes the possibility, at least for the present, of universal agreement in all cases. Consequently, the taxonomic status of border line populations will be determined to a large extent by a consideration of the other differentiating characters in addition to the one showing the greatest divergence. Leaving gaps between the proposed

limits of our taxonomic units thus allows leeway for the exercise of judgment in border line cases.

The necessity of exercising judgment in regard to populations falling near an arbitrarily fixed border line is shown by two pairs of populations cited above as illustrative examples, namely, the populations of *Sciaenops ocellatus*, and those of *Hippocampus hudsonius* (including all populations of the typical subspecies). Both pairs intergrade approximately by 30%. The intergradation of the latter pair is even a fraction greater in the samples examined. Nevertheless, the latter two populations are recognized as subspecies, and the former as races only for the following reasons: (1) Speciation in *Hippocampus* is rather unlike the usual. The species generally approach closely or even overlap (see Ginsburg 1937, p. 558 and *passim*). *Hippocampus* constitutes one of those groups in which different arbitrary lines between the categories will possibly have to be drawn in order to adequately represent the essential facts, as suggested on page 276. (2) The sampling of the two respective pairs of populations is not strictly comparable. Of *Sciaenops ocellatus* two extreme populations are compared, while of *Hippocampus hudsonius* intermediate populations are also included. Of the latter species, when the extremes are compared (see p. 268), the intergradation, 27%, falls within the arbitrarily fixed gap between the subspecies and the race as defined on page 260, and is less than in the extreme populations of *Sciaenops ocellatus*. (3) The populations of *Hippocampus hudsonius* diverge to a considerable extent in a number of other characters also, such as the number of dorsal rays, the number of pectoral rays, the relative length of the snout and the relative depth. (For a more detailed discussion of their differences see Ginsburg 1937, p. 557.) While the degree of intergradation in every character is considerable, an appraisal of the sum total of all the differences between the populations makes it evident that it is desirable to recognize them as subspecies rather than races. But for the populations of *Sciaenops ocellatus* no other well marked diverging characters are known at present.

The foregoing paragraph discusses some of the many factors involved which need to be considered in forming a final conclusion in regard to the status of a given pair of populations under study. A decision becomes especially difficult in cases where the samples available are manifestly inadequate, a frequent contingency in taxonomic practice. In such cases it would take an experienced, able and careful taxonomist, one who has a highly developed intuitive capacity, to form a decision which may stand the test of time and further, more adequate research. Even under the most favorable circumstances opinions regarding the rank of a given pair of populations may change as other, more divergent, characters are discovered. For instance, it is possible that some other characters may be discovered by which the populations of *Sciaenops ocellatus* may be shown to diverge to such a degree as to constitute subspecies.

The arbitrary lines suggested in this first attempt are admittedly tentative; but I believe that they approach closely to those which may be fixed after more extensive studies. Furthermore, any arbitrary line, no matter on how many concrete examples it may be based, will be from its very nature only generally indicative since all characters have to be considered in determining the taxonomic status of a pair of populations, as stated. Also, their proper use will always depend on the experience and ability of the taxonomist. Nevertheless, although the arbitrary lines here proposed are tentative, they are manifestly preferable to the rule of the thumb by which taxonomists now seem to decide regarding the category of particular pairs of populations. At least, they form a basis for immediate practice, as a general guide for taxonomists to determine whether any given pair of diverging populations are to be assigned specific, subspecific or racial rank. They also form a basis for discussion, improvement and refinement.

Irrespective of the question of the adequacy of the arbitrary lines here

TABLE XVII.
Some commonly used statistics of the populations discussed above,¹⁰ based on the data presented in Tables II-XV.

Population	M	R	σ	N	E_M^{11}	M_1-M_2	E_D^{11}	$M_1-M_2^{11}$	
								E_D	E_D
<i>Cynoscion regalis</i> , Chesapeake Bay	27.3750	5	.8856	40	.0944				
" " Florida coast	27.2727	5	.8833	110	.0568	.1023	.1102		0.9
<i>Cynoscion nebulosus</i> , Texas coast	25.4231	5	.7929	104	.0524				
" " Chesapeake Bay	25.2222	5	.8089	108	.0525	.2009	.0742		2.7
<i>Bairdiella chrysura</i> , Chesapeake Bay	21.2714	5	.8770	70	.0707				
" " Texas coast	20.8169	4	.7564	71	.0605	.4545	.0931		4.9
<i>Fundulus confluentus</i> , Florida coast	10.0000	3	.4000	25	.0540				
" " Norfolk, Va.	9.6034	2	.4892	58	.0433	.3966	.0692		5.7
<i>Hippocampus zosterae</i> , Key West, Fla.	9.8571	3	.4666	21	.0687				
" " Pensacola, Fla.	9.4615	2	.4985	13	.0933	.3956	.1159		3.4
<i>Leiostomus xanthurus</i> , Chesapeake Bay	30.7901	4	.8566	81	.0642				
" " Texas coast	30.0777	6	.8889	103	.0591	.712	.0873		8.2
<i>Sciaenops ocellatus</i> , Texas coast	24.6161	4	.7820	112	.0498				
" " Chesapeake Bay	23.7596	5	.7658	104	.0507	.8565	.0711		12.0
<i>Hippocampus hudsonius</i> ¹²	36.8451	5	.9442	71	.0756				
" " punctulatus ¹²	35.8462	5	.9484	26	.1255	.9989	.1465		6.8
<i>Cynoscion regalis</i> ²	27.2579	5	.8595	190	.0421				
" " arenarius ²	25.8739	5	.7510	119	.0464	1.3840	.0627		22.1
<i>Hippocampus zosterae</i>	12.0577	4	.5689	52	.0532				
" " regulus	10.9565	3	.3585	23	.0504	1.1012	.0733		15.0
<i>Gobionellus shufeldti</i>	12.9459	3	.3243	37	.0360				
" " boleosoma	12.0123	3	.2937	81	.0220	.9936	.0422		22.1
<i>Paralichthys lethostigma</i> ¹³	68.2222	15	2.2235	153	.1212				
" " albigitta	58.7387	11	2.0565	111	.1317	9.4835	.1790		53.0
<i>Gobiosoma bosci</i>	1.7765	0.5	.1002	17	.0164				
" " robustum	1.3438	0.4	.1059	16	.0159	.4327	.0243		17.8
<i>Lepidogobius guaymasiac</i>	24.4528	5	.7286	106	.0477				
" " y-cauda	21.1250	3	.6398	40	.0682	3.3278	.0832		40.0
<i>Paralichthys dentatus</i>	16.1826	6	1.1079	115	.0697				
" " lethostigma	9.4863	4	.6541	146	.0365	6.6963	.0787		85.1

proposed, the fundamental thing to remember is that no matter where drawn, the lines must be arbitrary. This is proved by the gradual series here presented. It is either one or the other. Either the different categories have no existence in fact, and in that case our use of the terms "species," "subspecies," "race," etc., should be abandoned. Or, if the categories do exist in nature, they can be based only on relative degrees of divergence. The sum total of experience obtained as a result of careful population studies made up to now unmistakably shows that the latter interpretation represents the true state of affairs in nature.

COMPARISON BETWEEN THE SIMPLE METHOD EMPLOYED IN
THIS PAPER AND THAT IN GENERAL USAGE.¹⁴

Attention has been called previously (p. 256) to the use of the standard method for comparing closely related populations as represented by the formula $\frac{M_1 - M_2}{\sqrt{E_1^2 + E_2^2}}$. This formula is not well adapted for our purpose, as may be shown by a consideration of the several factors which go to make up that expression.

First of all it may be stated that theoretically this expression in reality is not a measure of divergence. Rather, it is meant to be a test indicating, from a strictly mathematical point of view, the probable reliability of a difference between two sets of data, and consequently the probable value of any conclusions which may be drawn from such data. From a biological point of view, the usefulness of this test is limited in such a problem as we are confronted with. Since differences between populations exhibit all degrees of extensiveness, it follows as a consequence which can hardly be doubted that some average differences between natural populations exist, which are of such low magnitude as to be below the usually accepted mathematical "significance" obtained by the use of the above formula with samples which are ordinarily limited in practice. Such small differences must have a biological significance, although mathematically their significance appears doubtful. This test merely serves as a warning to proceed with caution in drawing conclusions in cases where the values are low, but it does not prove that such low values do not have any biological significance. However, while the above expression is strictly speaking not a measure of divergence, it may be used for that purpose. It is evident that, in general, the greater the divergence between two populations the greater is the numerical

¹⁴ See also footnote to Table XVI, p. 275.

FOOTNOTES TO TABLE XVII.

¹⁰ The symbols at the head of the columns stand for the following: M = arithmetical mean; R = actual range of the distribution on the X-axis; σ = standard deviation; N = number of specimens in composite sample; E_M = probable error of the mean; $M_1 - M_2$ = difference between the means of the two populations compared; E_D = probable error of $M_1 - M_2$.

¹¹ Biological statisticians are now generally employing the standard error instead of the probable error. To reduce the figures given in this table to the standard error and the derivatives based on it, divide the probable error of the mean, and the probable error of the difference between the means by the modulus .6745, and multiply the figures in the last column, showing "significance," by the same number. The relative magnitudes of the comparative figures given in the last column will thus remain the same.

¹² The sampling of the populations of *H. hudsonius* is not altogether comparable with those of *S. ocellatus*, as discussed on page 277. The statistics for the extreme northern population of the former (see Table VIII, p. 268) are: M = 37.0556; σ = 1.0787; E_M = 0.1213; and as compared with the southern population, *punctulatus*, $M_1 - M_2$ = 1.2094, E_D = .1745 and $\frac{M_1 - M_2}{E_D}$ = 6.9, or nearly the same as when the total sample of *hudsonius* is compared with *punctulatus* (see discussion on p. 280).

¹³ Omitting the one specimen at the extreme right of the frequency distribution (see Table XII, p. 271), the statistics for *lethostigma* are: M = 68.1645; R = 11; σ = 2.1134; E_M = 0.1156; and as compared with *albigutta* $M_1 - M_2$ = 9.4258; E_D = 0.1752, and $\frac{M_1 - M_2}{E_D}$ = 53.8.

value of this expression. Consequently, by the use of the above formula comparative figures are obtained which may indicate the relative degree of divergence of a pair of populations in a given series of pairs investigated. The question remains how useful is the standard method for our present practical purpose.

It will be noted that the above expression depends on: (1) the difference between the means which may be determined directly from the data by a simple arithmetical process of averaging, and (2) on the probable error which depends, in its turn, on a number of factors. The statistical formulae for the determination of the probable error are as follows:

$$\text{probable error of the mean} = .6745 \frac{\sigma}{\sqrt{N}}$$

$$\text{while, } \sigma \text{ (standard deviation)} = \sqrt{\frac{\sum f x^2}{N}}$$

The probable error then depends on the number of specimens in the composite sample and on the value of sigma. Now, the magnitude of sigma is determined primarily, (1) by the extent of the spread of the frequency distribution, the greater the spread the greater its value; and (2) by the form of the distribution; one having a sharply pronounced mode with the number of specimens diminishing rapidly at either end will show a comparatively smaller value for sigma, while a distribution the curve of which has a flattened form, or is skewed, will show a relatively greater value. (I am not considering very irregular distributions which may be due to faulty sampling, heterogeneity of the material or other causes.) It follows therefore that the value of the probable error depends chiefly on three factors, namely, (a) the number of specimens in the composite sample, (b) the spread of the distribution, and (c) the form of the distribution. Some of the factors involved are shown in Table XVII. The influence of the form of the distribution on the value of sigma is well shown by the two populations of *Fundulus confluentus*, for instance.

With these brief remarks we may now compare the method employed herein with the standard method. The final values obtained by these two methods are shown conveniently in parallel columns in Table XVI, page 274. Turning back to that Table it will be noted that of the 15 pairs of populations compared 10 occupy the same relative position by both methods, while 5 would occupy different positions if they were to be arranged in regular order by the standard method. A consideration of the latter cases throws considerable light on the relative merits of the two methods.

The first value out of place is that of *Hippocampus zosterae*, that obtained by the standard method being too low. The chief reason for the low value is shown in Table XVII. The composite samples are quite small, which results in a comparatively greater value for the probable errors. Although the spread of the distribution, and hence sigma, is small, its effect is not sufficient to counteract the influence of the small sample. On account of the relatively large probable error combined with the comparatively small difference between the means, the final expression obtained is relatively low.

The effect of the high probable error as a result of a small sample is also shown by the relatively low value obtained in comparing *H. punctulatus*, with *H. hudsonius*. Although in this case the sample of only one of the two populations compared is quite small and the difference between the means is higher, the effect of the small sample of the one population is sufficient to result in a low value.

The influence of the size of the sample on the final figure used for comparison is shown further by two different comparisons of the populations of *H. hudsonius*. The northernmost population of *hudsonius*, diverges to a greater extent than the populations from intermediate localities. from the

southernmost populations, *punctulatus*₁, (see Table VIII, p. 268). The two comparisons of these populations here made are as follows: (1) The intermediate populations are grouped with the northern one into the subspecies *hudsonius*₂ and the composite sample is compared with the southernmost populations, designated as the subspecies *punctulatus*₂ (see Table XVII, p. 278). (2) The northernmost population only of *hudsonius*₁ is compared with the southernmost ones, *punctulatus*₂ (see footnote to Table XVII). The "significant" figures obtained in these two comparisons are about the same, 6.8 and 6.9, respectively. The greater divergence of the populations from near the extremes of the geographic range of the species as a whole, is not indicated by these figures. The same two comparisons made by the method here employed are 30% and 27%, respectively, which does show the lesser intergradation, or greater divergence, of the populations from the extremes of the geographic range. The figures obtained by the use of the standard formula fail to show this greater divergence, evidently because the number of specimens in one of the composite samples used in the second comparison is considerably less than that in the first comparison.

On the other hand, the value for the comparison between *Cynoscion regalis*₂ and *C. arenarius*₂ is relatively high and for the same reason. In this case the samples are comparatively large, resulting in a low probable error, and this combined with the rather large difference between the means gives a relatively high figure as the final result. The magnitude of the figure obtained by the standard method in comparing a pair of related populations is thus greatly influenced by the number of specimens in the samples; but by far not to such an extent by the method employed.

The influence of the figure representing the probable error may also be shown by the following hypothetical examples. Let us suppose that of population A we study a sample n_1 which is sufficiently representative for all practical biological purposes. Let us now take another sample n_2 of the same population containing say ten times the number of specimens in the first sample. Biologically, as far as we may draw any conclusions from their study, the two samples are very nearly alike; but mathematically the probable error of the second sample will be smaller. Of course, this is perfectly logical. It simply shows that from a mathematical point of view the reliability of the sample increases as the number of specimens is increased. However, from a practical biological point of view let us see what will happen when population A is compared with another population. Let us suppose that we take a sufficiently representative sample m of a population B. If now we compare sample n_1 with m we will get one figure; while by comparing n_2 with m we will get a different and, quite likely, a widely divergent figure. Two separate comparisons of population A with B will thus yield two results.

In general, as n increases the numerical value of
$$\frac{M_1 - M_2}{\sqrt{E_1^2 + E_2^2}}$$
 will increase. Consequently, the standard formula in the form in which it is generally employed is not suitable for the practical purpose of obtaining a series of comparative figures. On the other hand, by the method employed here the results will differ but little with the size of the samples, especially when such composite samples give fairly approximate representations of their populations.

Of even greater importance in comparing the two methods is the factor $M_1 - M_2$. It is obvious that pairs of populations the chief differentiating characters of which are not the same or in which the values of $M_1 - M_2$ differ widely can not be fairly compared by any method employing this factor. A striking effect of the influence the factor $M_1 - M_2$ exerts on the final value obtained by the standard method, is shown by the comparison between *P. lethostigma* and *P. albigutta*. The difference between the means in this case is comparatively high, resulting in a very high value for the final figure, although the probable error is also high because of the wide spread of the

distribution. In spite of the fact that this pair of populations shows a slight amount of intergradation, the index of their divergence obtained by the standard method is much greater than that of other pairs which do not intergrade at all. This example shows in a striking manner that the standard method is not well adapted for our purpose which requires the comparison of pairs of populations that differ by widely unlike characters.

The influence of the factor M_1-M_2 is further shown by the comparison of the fifth pair of populations falling out of line, namely, that of *Gobiosoma bosci* and *G. robustum*. In this case, although the samples are small, nevertheless the probable error is relatively small, evidently because of the small range, according to the unit adopted. In spite of the small probable error, the final figure obtained is yet relatively small, evidently due to the small difference between the means.

It is evident that the standard formula is not well adapted for our purpose because the several factors involved do not result in fair comparative figures. It is preferable from the point of view of theoretical mathematics in determining probabilities; but for our purpose it is all too often not practically workable. One great drawback is that in practice we usually do not have samples of sufficient size that may be adequate according to mathematical usage. But irrespective of the size of the samples, the formula is not properly applicable because of the other factors involved, as discussed above. An application of the standard formula evidently is often bound to lead us astray. Although the method employed lacks the mathematical elegance of the standard method, in reality it gives a truer picture and interpretation of the facts of nature in connection with the problem under consideration. The relative degree of divergence of the pairs of populations, or their position in the series, with which this paper deals, is shown more nearly in keeping with the facts of nature or more accurately by our present method.

The method here employed also has the advantage of greater clarity. In using the standard formula biometricians seem to be chiefly concerned whether the resulting figure is "significant" or not; but once "significant" figures are obtained no particular stress seems to be laid generally on the relative value of figures of differing magnitude. For instance, let us say that we compare three pairs of populations and obtain the three "significant" figures of 5, 10 and 15, respectively. Now, definitely, just what is the meaning of these relative figures outside their implication of differing degrees of probability? Certainly, this is not clear to the average busy biologist. Of course, 5 is greater than 10, and 10 is greater than 15; but the differences between these figures do not convey any special meaning or idea in connection with our problem, since the biologist is not in the habit of thinking in such terms. Indeed, the relative magnitude of such figures hardly seem to have any definite meaning within rather wide limits even to the statisticians. Furthermore, such figures are not susceptible of conveying a very precise meaning with respect to divergence; because their value changes materially as the size of the sample is changed, and with other factors. Even their relative value in the series is likely to change with a change in these factors. On the other hand, by the method employed, if we compare three pairs of populations and find that the intergrades are 5, 10, and 15 per cent, respectively, of the total number of individuals in the composite samples, on the average, such figures immediately convey a definite and clear meaning to every biologist.

NOMENCLATURE OF TAXONOMIC UNITS BELOW FULL SPECIFIC RANK.

It has been shown that the boundary lines which may be drawn between the species and its subdivisions are arbitrary, and tentative limits have been proposed where to draw such lines. The nomenclature of the species and

its subdivisions may now be considered with profit, and a simpler method than the one now in use is here proposed.

According to present usage which is sanctioned by the international code of zoological nomenclature, subspecies are designated in the form of trinomials. The international code goes into the subject only as far as subspecies are concerned, and no units of lower rank are considered; but on account of the arbitrary nature of these categories there is no fundamental reason for stopping there, and some authors now are using quadrimomials, generally inserting the term "variety" between the third and fourth words of the full name. However, there is likewise no reason for stopping even there. One, conceivably, may even propose to use quinquinomials, sexinomials, etc., since in a gradual series such as we are dealing with where the boundary lines necessarily must be arbitrary, such boundaries may be increased.

It is evident that carried to its logical conclusion, the nomenclature of taxonomic units below specific rank would become clumsy and unwieldy, and assume a form very similar to the pre-Linnaean polynomial nomenclature; although it is true that the fundamental nature of the binomial system would be retained. It is evident, therefore, that there is room for improvement in our present method of naming taxonomic units below specific rank.

Another practical difficulty inherent in the present system is found in the relation of zoological considerations to nomenclature. It should be remembered that the Linnaean or binomial system of nomenclature serves two virtually independent purposes: (1) It supplies names to species and groups of higher or lower rank, such names being for the practical use of handles by which we may discuss these entities. (2) It also attempts to show relationship. In practice these two purposes cannot be made to work in entire accord. For the first purpose stability is a primary consideration, and it could be served most effectively by a set of arbitrary rules, such as the international code; but since the second purpose must also be considered, absolute stability is impossible, and part of the full names of organisms must change with increased knowledge, with our changing ideas of relationship, or with differences in the interpretation of relationship by individual biologists. Changes in nomenclature caused by zoological considerations are, or may be, chiefly of two kinds.

First, changes in the first word or the generic part of the name of a species are caused by the everlasting shifting about of species from one genus to another, or the frequent changing of the boundaries of genera by individual zoologists. Species are thus constantly shuffled with respect to their generic affiliations. Nomenclatorial instability of this kind is, of course, inherent in the system and is frequently unavoidable; although it would be well for zoologists to exercise restraint in their treatment of many cases of this kind by refraining from changing the constitution of genera on the slightest provocation.

Second, in genera in which the populations are now in an early and active state of diversification and ramification, questions may arise: (a) as to whether a given population is to be properly assigned specific or subspecific rank, and (b) if the latter, as to the proper species into which it is to be grouped. In such cases, any interpretation given of the relationship between closely related populations, on the basis of the available zoological evidence, is not the only possible one. The chief difficulty in the way of a single, consistent and acceptable interpretation in cases of this kind often lies in the uncertainty as to which one of the several populations is the more primitive one, and the consequent uncertainty as to the starting point of the argument. This is primarily due to our present very imperfect knowledge of the mechanism and methods of descent. While the available evidence may show to a high degree of probability that the several populations under consideration

should be assigned to taxonomic units of varying degree, yet the interpretation of their relationship on which such assignment must depend is of a speculative nature to a large extent. Examples of such genera are *Hippocampus* (see, for instance, page 549 of my review, 1937), and *Bathygobius* (a study of which I have now prepared in manuscript form). In such cases scrambling and unscrambling of the trinomial names of subspecies may well be expected to result from different interpretation of the data by individual zoologists.

In view of the possible resulting complexity of nomenclature as outlined above, the impossibility of being reasonably certain of relationship, in some cases, at the present time, and the necessarily arbitrary nature of limiting taxonomic units, the following method of naming species and their subdivisions is here proposed. All names are to be binomial. To indicate that a taxonomic unit is to be regarded as a full species the numeral 1 is inserted after the specific name of the binomial; a taxonomic unit of the next lower rank is to have the numeral 2 inserted in the same place; the next lower, the figure 3. Related populations of organisms of the rank of full species or lower are thus divided by arbitrary lines into categories and the categories designated by number, namely, a category of the first order or a full species, a category of the second order or a subspecies, a category of the third order or a race. In the case of a full species which is not subdivided the numeral may be left out in writing its binomial designation. By way of illustration, a taxonomic unit of the second category would be designated as:

$$A - us \quad a - us_2;$$

while a unit of the third category would bear the designation:

$$A - us \quad b - us_3.$$

The subspecies treated of in this paper are designated above according to the proposed method.

The proposed method is in consonance with the international code, except for the required use of trinomials for subspecies, which is not universally followed anyway. If anything it will tend to reenforce the system of binomial nomenclature which will thus become binomial in fact as well as in theory, and the necessity for using the clumsy trinomial and quadriminomial designations will be obviated. Another advantage is that this method does not imply a commitment as to the relationship of the populations named. It has already been pointed out that given a certain set of evidence relationship may be interpreted sometimes in more than one way. In such cases, if the nomenclature be used in the form here proposed it will be in accordance with the known facts and no more; the probable taxonomic rank of the particular unit may thus be indicated without the necessity of making a commitment in regard to relationship about which one may be uncertain.

An apparent advantage of this method of nomenclature is its flexibility. However, its very flexibility may turn out to be a disadvantage if the method is not used with caution. It may tend to put a premium on careless work. Without the necessity of using trinomials, quadriminomial, etc., it may result in the excessive multiplication of new names based on unimportant or irrelevant differences exhibited by a few specimens after a haphazard examination of such specimens. Nevertheless, the advantages of this method are so evident that they outweigh this possible disadvantage, and, in any case, there is no absolute insurance against careless or half-baked work. The undesirable contingency indicated may be obviated by a general agreement among systematists to refrain from formally naming categories of a rank lower than a subspecies, or at least the next lower or third category which would be equivalent to a quadriminomial as now used; otherwise the resulting great increase in new names will tend to make zoological nomenclature too burdensome.

SUMMARY.

1. No absolute criterion exists by which to determine just what is a species. All proposed criteria hold only in part or in special cases. Morphology is the only practical and most generally applicable criterion, although it has only a relative value. The present study is based entirely on that criterion.

2. Intergradation in nature is universal. It is the rule rather than the exception. This is true of species as well as of subspecies or taxonomic categories of lower rank. (To a certain extent this is also true of categories higher than species, but this paper deals only with the species and its subdivisions.) Consequently the limitation of the species concept or that of any of its subdivisions must depend on the *degree* of intergradation.

3. The intergradation between, or the divergence of, natural populations is such that if some method be adopted for measuring intergradation, or divergence, and a sufficient number of pairs of closely related populations be compared, the figures expressing the measures and indicating the degree of intergradation, or divergence, will form a continuous series without any breaks. Consequently, it follows that any limitation given to our concept of species, subspecies, race, etc., necessarily must be arbitrary.

4. A definite measure which is determined by a simple arithmetical calculation is employed in the present study for the purpose of expressing intergradation, or divergence. This measure is based on the character showing the greatest divergence between the two populations.

5. The measure employed has the advantage of simplicity, clarity and ease of determination, and it gives a correct though approximate interpretation of the data.

6. Using this measure as a basis, definitions of the terms species, subspecies, and race are presented.

7. The necessity of proper sampling of the material from which the data are obtained, that form the basis of the measure, is indicated and discussed. The method of sampling the material used in the present study is stated.

8. A series of examples of pairs of related populations of fishes is presented, showing the application of the measure, proving the gradualness of intergradations, *inter se*, and showing that the necessarily arbitrary boundaries drawn in the definition of the species and its subdivisions, are more or less in accordance with the facts of speciation as they occur in nature.

9. A comparison is made between our method of measuring divergence and the standard method.

10. A method for the nomenclature of populations below specific rank is proposed.

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¹⁵ Includes only those publications to which reference is made in the text.